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Soil methane oxidation in both dry and wet temperate eucalypt forests shows a near-identical relationship with soil air-filled porosity

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Abstract. Well-drained, aerated soils are important sinks for atmospheric methane (CH₄) via the process of CH₄ oxidation by methane-oxidising bacteria (MOB). This terrestrial CH₄ sink may contribute towards climate change mitigation, but the impact of changing soil moisture and temperature regimes on CH₄ uptake is not well understood in all ecosystems. Soils in temperate forest ecosystems are the greatest terrestrial CH₄ sink globally. Under predicted climate change scenarios, temperate eucalypt forests in south-eastern Australia are predicted to experience rapid and extreme changes in rainfall patterns, temperatures and wild fires. To investigate the influence of environmental drivers on seasonal and inter-annual variation of soil–atmosphere CH₄ exchange, we measured soil–atmosphere CH₄ exchange at high-temporal resolution (< 2 h) in a dry temperate eucalypt forest in Victoria (Wombat State Forest, precipitation 870 mm yr⁻¹) and in a wet temperate eucalypt forest in Tasmania (Warra Long-Term Ecological Research site, 1700 mm yr⁻¹). Both forest soil systems were continuous CH₄ sinks of $-1.79 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ in Victoria and $-3.83 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ in Tasmania. Soil CH₄ uptake showed substantial temporal variation and was strongly controlled by soil moisture at both forest sites. Soil CH₄ uptake increased when soil moisture decreased and this relationship explained up to 90 % of the temporal variability. Furthermore, the relationship between soil moisture and soil CH₄ flux was near-identical at both forest sites when soil moisture was expressed as soil air-filled porosity (AFP). Soil temperature only had a minor influence on soil CH₄ uptake. Soil ni-

trogen concentrations were generally low and fluctuations in nitrogen availability did not influence soil CH₄ uptake at either forest site. Our data suggest that soil MOB activity in the two forests was similar and that differences in soil CH₄ exchange between the two forests were related to differences in soil moisture and thereby soil gas diffusivity. The differences between forest sites and the variation in soil CH₄ exchange over time could be explained by soil AFP as an indicator of soil moisture status.

1 Introduction

Methane (CH₄) has a relatively low atmospheric concentration of approximately 1.8 ppm and is, after carbon dioxide (CO₂, approx. 402 ppm), the second most abundant greenhouse gas in the atmosphere (IPCC, 2013). Although its atmospheric concentration is 2 orders of magnitude lower than that of CO₂, CH₄ accounts for approximately 18 % of the currently observed global temperature increase (IPCC, 2013). In addition, CH₄ contributes to 32 % of the current radiative forcing created by the major greenhouse gases as it has a 25 times greater global warming potential compared to CO₂ (IPCC, 2013).

Forest soils are the most important land-based sink for CH₄ via the activity of methane-oxidising bacteria (MOB) in well-drained, aerobic soils. Soils in temperate forest ecosystems play an important role in global CH₄ exchange between the land mass and the atmosphere and they constitute around

30–50 % of the soil-based CH₄ sink worldwide (Ojima et al., 1993; Dutaur and Verchot, 2007).

Major environmental factors controlling and influencing CH₄ uptake rates by forest soils are soil diffusivity, soil structure, soil moisture, soil temperature and soil nitrogen status (Ball et al., 1997; Smith et al., 2003; von Fischer and Hedin, 2007; Butterbach-Bahl et al., 2002; Del Grosso et al., 2000).

The main factor regulating the CH₄ uptake capacity of soils is the diffusion rate of CH₄ through the soil and hence the substrate availability of CH₄ to the MOB across the soil profile. CH₄ uptake rates have been shown to decrease with increasing soil moisture as a result of decreasing soil gas diffusion rates across different ecosystems (Castro et al., 1995; Khalil and Baggis, 2005; Ball et al., 1997). Therefore, CH₄ uptake is thought to be most rapid in coarse-textured forest soils with a well-developed structure and an organic surface layer that does not inhibit gas diffusion (Boeckx et al., 1997; Del Grosso et al., 2000; Smith et al., 2000). Soil bulk density can also correlate with soil CH₄ uptake across different ecosystems (Smith et al., 2003, 2000), which is not unexpected since soil air-filled porosity, which is directly linked to soil diffusivity, is a function of soil bulk density and volumetric water content.

Soil CH₄ uptake at atmospheric levels generally shows limited temperature dependency and reported Q_{10} values are generally low with an average around 1.4 (Crill, 1991; Born et al., 1990; Smith et al., 2000). Another factor that influences the CH₄ uptake capacity of soils is soil N status, especially the availability of ammonium (NH₄⁺) (Butterbach-Bahl et al., 1998; Sitaula et al., 1995). Increasing soil N availability through organic and inorganic fertiliser additions and through biological N fixation can decrease CH₄ uptake rates (Niklaus et al., 2006; Dick et al., 2006).

Temperate eucalypt (broadleaved evergreen) forests in south-eastern Australia cover around 26 million hectares (Montreal Process Implementation Group for Australia and National Forest Inventory Steering Committee, 2013) and provide a large range of ecosystem services. However, despite a growing interest in soil CH₄ uptake in the last decade there have been very few studies investigating CH₄ oxidation in soils of natural Australian forest and woodland ecosystems, with only a relatively small number of published studies on CH₄ uptake in temperate forest systems (Livesley et al., 2009; Meyer et al., 1997; Fest, 2013; Fest et al., 2009, 2015a, b), tropical forest systems (Kiese et al., 2003) and savanna ecosystems (Livesley et al., 2011). Moreover, there is currently no model that accurately predicts the size of the terrestrial CH₄ sink in Australia or determines how the strength of this sink will change over time. Data describing CH₄ emission and oxidation from Australian soils is still patchy and often lacking for important landscapes such as tropical savannas, the semi-arid and arid zones and woody ecosystems (Dalal et al., 2008).

Compared to most European and North American temperate forest systems, forest soils in the Australian temperate

region are generally highly weathered and very low in nutrients and atmospheric nitrogen deposition is very low. Furthermore most of the temperate forest area in Australia does not experience periods of snow cover or below zero soil temperatures. It is therefore questionable as to whether information gathered on spatial and temporal variability of soil CH₄ exchange in Northern Hemisphere temperate forest soils are transferable to those in Australia. Furthermore, it is not clear if processes that explain soil CH₄ uptake in deciduous forest systems or coniferous forest systems worldwide can be directly transferred to the eucalypt or acacia forest systems that dominate the forests and woodlands of Australia. Most estimates of soil CH₄ exchange in Australian forest systems were based on infrequent (weekly–monthly) or campaign-based measurements (of 1–2 weeks), which may not fully reflect the temporal dynamics and range of environmental conditions.

This study investigates soil–atmosphere CH₄ exchange using automated chamber systems measuring at a high-temporal resolution over 1–2 years in two temperate *Eucalyptus obliqua*-dominated forest sites with contrasting annual precipitation. The main objectives of this study were to assess the magnitude and temporal variation in CH₄ exchange between the soil and atmosphere in temperate evergreen eucalypt forest systems and to investigate the primary biophysical processes that control the seasonality in soil CH₄ flux.

2 Material and methods

2.1 Site description

The Tasmanian site is in the Warra Long-Term Ecological Research (LTER) site approximately 60 km west-southwest of Hobart, Tasmania, Australia (AU-WRR: 43°5′36.78″ S, 146°38′42.65″ E). The site is dominated by *Eucalyptus obliqua* (L’Her.) with an overstorey height of around 53 m and a basal area of 54 m² ha⁻¹. The understorey is mainly comprised of *Acacia melanoxylon* (R. Br.), *Nothofagus cunninghamii* (Hook.) Oerst. and *Dicksonia antarctica* (Labill.). The climate of AU-WRR is classified as temperate cool wet (Dunlop and Brown, 2008) with cold and wet winters and warm and wet summers. The average rainfall is approximately 1700 mm yr⁻¹ (Fig. 1a) with mean monthly maximum temperatures of 19.3 °C in January (summer) and mean minimum temperatures of 2.5 °C in July (winter). The soils at Warra are derived from Permian siltstone with a surface texture of silty loam to silty clay loam and are classified as Kurosolic Redoxic Hydrosol (McIntosh, 2012). The average bulk density in the top 5 cm of mineral soil is 0.67 g cm⁻³ and soil porosity is 0.74 cm³ cm⁻³.

The Victorian forest site is in the Wombat State Forest, approximately 120 km west of Melbourne, Australia (AU-WOM: 37°25′20.83″ S, 144°5′38.63″ E). AU-WOM is dominated by *Eucalyptus obliqua* (L’Her.), *Eucalyptus rubida* (H.

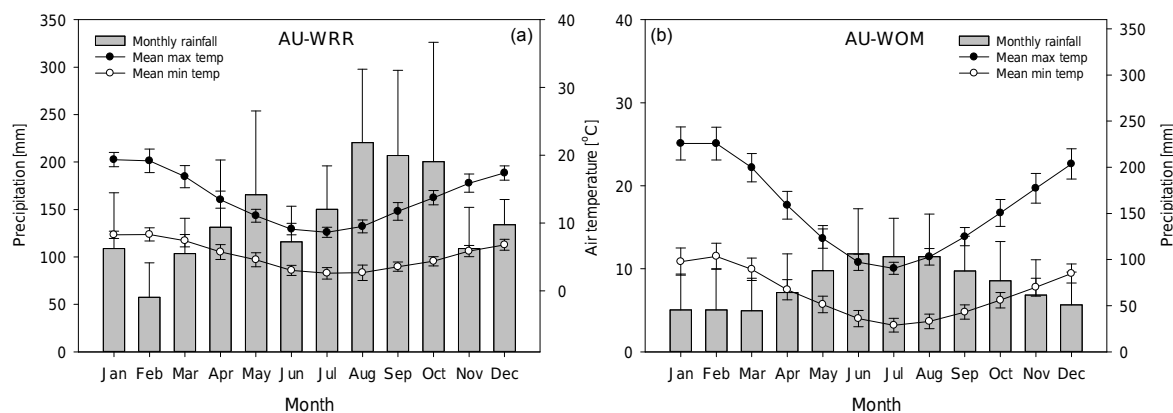


Figure 1. Climate at the investigated sites of (a) Warra Long-Term Ecological Research in Tasmania (AU-WRR) and (b) Wombat State Forest in Victoria (AU-WOM). Black circles represent monthly mean maximum air temperatures. White circles represent monthly mean minimum air temperatures. Grey bars represent monthly precipitation. Error bars represent ± 1 SD. Data source: Bureau of Meteorology Australia, <http://www.bom.gov.au> (station numbers 097024 for AU-WRR and 088020 for AU-WOM).

Deane & Maiden) and *Eucalyptus radiata* (Sieber ex DC.) trees of approximately 20–25 m in height and $37 \text{ m}^2 \text{ ha}^{-1}$ of stem basal area. The climate is classified as Mediterranean to cool temperate, with warm and dry summers and wet and cool winters. The average rainfall is approximately 870 mm yr^{-1} (Fig. 1b) with mean monthly maximum temperatures of 25.6°C in January (summer) and mean minimum temperatures of 3.4°C in July (winter). The soils of AU-WOM are derived from weathered sandstone and shale, with a surface texture of sandy clay loam, classified as an acidic-mottled, dystrophic, yellow Dermosol (Robinson et al., 2003). The average bulk density in the top 5 cm of mineral soil is 0.90 g cm^{-3} and soil porosity is $0.65 \text{ cm}^3 \text{ cm}^{-3}$.

2.1.1 Experimental design AU-WRR

The temporal variation in soil–atmosphere exchange of CH_4 was monitored continuously from 10 October 2010 to 15 January 2012 using a fully automated gas chromatograph (GC) measurement system attached to 10 pneumatic open-and-close chambers as described in Livesley et al. (2009). This system was supported by a remote area power system consisting of a 5 kW diesel generator and 12 V battery bank. The 10 chambers were randomly distributed over an area of approximately $25 \times 25 \text{ m}$. Chambers were attached to a square steel-frame base (e.g. $50 \times 50 \text{ cm}$) which was inserted 5 cm into the soil and a plexiglass headspace of 15 cm depth (e.g. 37.5 L chamber volume). Chambers were attached to the frame using clamps and closed cell foam. For each chamber, six flux rate measurements were made during a 24 h period, one every 4 h. Further details of the automated trace gas measurement system, chamber design and gas chromatograph can be found in Butterbach-Bahl et al. (1997), Papen and Butterbach-Bahl (1999) and Livesley et al. (2009). Soil temperature (12-Bit Temp Smart Sensor, Onset Computer Cooperation, USA) and moisture (EC-5 Soil Moisture Smart Sen-

sor, Onset Computer Cooperation, USA) was logged at 0–10 cm on a half-hourly basis (Hobo U30, Hobo Data Logger, Onset Computer Cooperation, USA) in the middle of the site. Chamber pneumatic lids opened automatically when rainfall, measured by a tipping bucket rain gauge, exceeded 1 mm in 5 min to avoid a potential reduction in soil moisture inside the chambers caused by the rainfall exclusion during the relatively long time of chamber closure (2 h).

2.1.2 Experimental design AU-WOM

Temporal variation in soil–atmosphere exchange of CH_4 was monitored continuously from 1 May 2010 to 30 April 2012 using a fully automated Fourier transform infrared (FTIR) spectrometer measurement system attached to six pneumatic open-and-close chambers (Griffith et al., 2012). This system was supported by a remote area power system consisting of a 4.5 kW diesel generator and 24 V battery bank. The automatic chambers used followed the same design as that described at the AU-WRR site. The opening and closing of the lids via pneumatic pistons was controlled with the measuring software on site (Spectronous Software, Ecotech PTY Ltd). Six chambers were distributed randomly over an area of around $25 \times 25 \text{ m}$ and were measured in sequence with each chamber initially having a measuring period of 15 min (1 May–21 October 2010) that was later extended to 20 min to increase detection precision for other simultaneously measured trace gases (22 October 2010–30 April 2012). Lids were open for both the first and the last 2 min of every 15/20 min measuring interval per chamber to flush the sample lines with ambient air, resulting in a chamber incubation period of 11/16 min. One CH_4 flux measurement per chamber was achieved every 1.5/2 h. The chambers were not fitted with a fan, but there was forced ventilation during the incubation period of each chamber through the use of an external pump which circulated the air in a closed loop through the

head-space of the chamber (closed dynamic set-up), attached airlines (0.3 L tubing volume) and the measuring cell (3.5 L cell volume) of a FTIR spectrometer set-up (Spectronus, Ecotech Pty. Ltd., Australia). The spectrometer (Bruker IR-cube with global source and thermoelectrically cooled mercury cadmium telluride detector) measured concentrations of CH₄, CO₂, N₂O, carbon monoxide and water vapour in the air stream (Meyer et al., 2001; Griffith et al., 2012; Hammer et al., 2013). Measurements of the CH₄ concentration were made every minute during the 15/20 min chamber period. Further information about measuring principle, instrument set-up, maintenance and calibration can be found in Griffith et al. (2012). Soil temperature (thermocouple probe) and moisture (impedance probes, ML2x – Theta Probe Soil Moisture Sensor, Delta-T Devices Ltd., UK) was recorded continuously at 0–5 cm within each chamber. In addition, soil temperature (Averaging Soil Thermocouple Probe, TCAV, Campbell Scientific Australia) and soil moisture (Water Content Reflectometer, CS616, Campbell Scientific Australia) were recorded on a half-hourly basis at 0–10 cm by an on-site eddy covariance system. Given the relatively short closure period of 11/16 min for each chamber during a 4 h period, we decided that automated chamber opening in response to rainfall events was not necessary.

2.2 Flux calculation

CH₄ flux rates were calculated for both automated measuring systems from the rate of increase/decrease of gas concentration in the chamber head space with time according to

$$F_{\mu\text{L}} = (V/A) \times (dC_{\text{CH}_4}/dt), \quad (1)$$

where V is the volume (L) of the chamber head space plus sample lines and the FTIR sample cell, A is the soil surface area covered by the chamber (m²) and t is time. The term dC_{CH_4}/dt (μL L⁻¹ h⁻¹) was calculated from the initial linear CH₄ concentration change after chamber closure. In cases where the fitted linear regression model had an $R^2 < 0.9$, this flux measurement was excluded from further analysis. The determined flux rate ($F_{\mu\text{L}}$) was subsequently converted to μmol CH₄ m⁻² h⁻¹ ($F_{\mu\text{mol}}$) by accounting for temperature, pressure and volume using Eq. (2) based on the ideal gas law:

$$F_{\mu\text{mol}} = (F_{\mu\text{L}} \times P)/(R \times T), \quad (2)$$

where P is the atmospheric pressure in kPa at site according to altitude or direct measurement (Eddy tower), R is 8.3144 (the ideal gas constant in L kPa⁻¹ K⁻¹) and T is the air temperature in kelvin (273.15 + °C). Fluxes in μmol CH₄ m⁻² h⁻¹ were then converted to μg CH₄-C m⁻² h⁻¹ based on the molecular atomic mass.

2.3 Additional measurements

From within each site, composite soil samples (three 0–5 cm samples) were collected, sieved (2 mm) and sub-sampled for

1M KCl extraction (1 : 4, soil : KCl) and gravimetric water content (GWC_S) determination (105 °C for 48 h) during additional seasonal measurement campaigns spread across the measurement time frame ($n = 13$ in AU-WOM, $n = 10$ in AU-WRR. KCl extracts were filtered (Whatman 42) and frozen prior to analysis for nitrate (NO₃⁻) and ammonium (NH₄⁺) concentration using an autoanalyser (SFA, Technicon™).

During initial site installation (and over the course of the measurement time frame), approximately 30 volumetric soil cores (0–5 cm, Ø 72 mm) were sampled at each site to determine soil volumetric water content (VWC) and soil bulk density (BD). The data were used to establish site dependent calibration curves between the on-site installed soil moisture sensors (HOBO Micro Station Data Logger H21 and EC-5 Soil Moisture Smart Sensor, Onset Computer Corporation, USA), hand-held impedance probes (ML2 × Theta probe and HH2 Moisture Meter, Delta-T Devices Ltd., UK) and VWC (Kaleita et al., 2005). The bulk density and volumetric water content data and their relationship to the on-site installed soil moisture sensor readings and hand-held impedance probes readings were further used to calculate soil porosity, air-filled porosity and percentage water-filled pore space (%WFPS) for each plot and measuring event according to Loveday and Commonwealth Bureau of Soils (1973) as follows:

$$\text{soil porosity} = 1 - (\text{soil bulk density}/\text{particle density}), \quad (3)$$

where a value of 2.65 was used for particle density (g cm⁻³) of rock, sand grains and other soil mineral particles;

air – filled porosity =

$$\text{soil porosity} - \text{volumetric water content}; \quad (4)$$

%WFPS =

$$(\text{volumetric water content} \times 100)/\text{soil porosity}. \quad (5)$$

At the end of the study, a composite soil sample from five soil cores was collected at 0–5 cm at each site, air dried, sieved (2 mm) and analysed for soil particle size analysis through dispersion, suspension, settling and sequential hydrometer readings (Ashworth et al., 2001). A sub-sample of each air-dried soil was analysed for pH (1 : 5, soil : water) and for total C and N content using an elemental analyser (LECO®).

2.4 Data presentation and statistical analyses

Flux and environmental sensor data presented (if not specifically related to individual chambers) in the figures here after are averages for respective chamber cycles where at least two-thirds of the chamber flux measurements had passed the above mentioned flux quality control (1.5/2 h cycle for the FTIR system and a 4 h cycle average for the GC system) at each site ±1 SE (where error bars are present). We also calculated the coefficient of variance per chamber cycle (CV%_{cycle}) by dividing the standard deviation of each chamber cycle by its respective mean and multiplying the result

Table 1. Parameters and coefficients of determination (Adj. R^2 is adjusted R-squared) of linear regression models explaining seasonal variability in mean chamber cycle methane flux (F_{CH_4}) at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria (AU-WOM) and at a mixed *E. obliqua* and *E. regnans* forest stand, Warra LTER, Tasmania, Australia (AU-WRR). Standardised coefficients β are in parentheses. SD refers to standard deviation of parameter; level of significance (* $p \geq 0.001$). Predictors: T_{S} (soil temperature), AFP (air-filled porosity) and soil VWC (volumetric water content). Presented constants are model intercepts and parameters represent the slopes for the predictor variables.

Site	Dependent variable	Constant	VWC (SD = 0.051)	T_{S} (SD = 1.98)	AFP (SD = 0.488)	Adj. R^2
AU-WRR	F_{CH_4} (SD = 10.899)	−92.307*	195.378* (0.925)	–	–	0.855*
	F_{CH_4} (SD = 10.899)	−19.543*	–	−2.215* (−0.399)	–	0.158*
	F_{CH_4} (SD = 10.899)	−88.835*	191.664* (0.907)	−0.254* (−0.046)	–	0.857*
	F_{CH_4} (SD = 10.899)	53.640*	–	–	−195.378* (0.925)	0.855*
		Constant	VWC (SD = 0.055)	T_{S} (SD = 3.42)	AFP (SD = 0.402)	Adj. R^2
AU-WOM	F_{CH_4} (SD = 11.296)	−75.068*	195.768* (0.957)	–	–	0.915*
	F_{CH_4} (SD = 12.720)	−6.320*	–	−1.701* (−0.458)	–	0.209*
	F_{CH_4} (SD = 10.607)	−78.336*	201.671* (0.982)	0.147* (0.047)	–	0.900*
	F_{CH_4} (SD = 11.296)	53.943*	–	–	−195.768* (0.957)	0.915*

by 100. Furthermore, soil temperature and soil moisture data were averaged accordingly for each chamber cycle to allow regression analysis. In a second step, to enable correlation analysis with daily rainfall and sporadic soil inorganic nitrogen measurements we calculated daily site averages of the measured fluxes and environmental parameters, with the exception of rainfall where we calculated daily sums, for days where at least 80 % of chamber cycles were available. In addition, we calculated the coefficient of variation per day ($\text{CV}\%_{\text{day}}$) for the CH_4 flux data. As outlined above, we excluded fluxes where the coefficient of determination of the regression of chamber concentration vs. time was less than 0.9, which lead to the exclusion of approximately 10 % of measured chamber fluxes. However, longer gaps in flux data, as shown in Figs. 1a and 2a, are either a result of power failures or the need to switch off the power generators on days of extreme fire danger. This led to data gaps in around 30 % of the individual datasets.

All statistical analyses were performed with SPSS 20 (IBM, USA). Linear regression procedures and multiple linear regression procedures were used to investigate temporal relationships between measured soil environmental parameters and soil CH_4 . We initially ran stepwise linear regression procedure as an exploratory tool to identify significant predictors and predictor combinations and retested these afterwards in simple or multiple linear regression models. We transformed data when necessary to reduce heteroscedasticity for linear regression analysis. We used a restricted maximum likelihood framework (REML; automatic linear modelling in SPSS) to arrive at the Akaike information criterion for three selected models that predict soil CH_4 uptake (one model containing only soil temperature, one model containing only a measure of soil moisture (we choose air-filled porosity, AFP) and one model containing soil temperature and AFP as a predictors of soil CH_4 flux.

2.5 Annual site CH_4 flux budgets

To calculate annual site CH_4 flux budgets for both sites we first selected a 12-month period with the greatest data coverage for daily average flux for both sites (1 January 2011–1 January 2012) and filled existing flux data gaps as follows. For small data gaps of single days where no environmental sensor or flux data were available, we calculated values based on linear interpolation between the CH_4 flux of the day before the gap and the day after the gap. For data gaps longer than 1 day, we used the linear regression model between soil VWC soil moisture and daily soil CH_4 flux for each site (Table 1) to estimate the missing CH_4 flux data.

3 Results

3.1 CH_4 flux in relation to soil environmental variables

At the AU-WRR site, soil CH_4 flux was always negative indicating CH_4 uptake all year round (Fig. 2). The measurement cycle means ranged between $-2 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ (spring 2010) to $-58.4 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ (autumn 2011) with an arithmetic mean of $-41.2 \pm 11.0 \text{ SD } \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$. In general, months with higher average soil moisture and higher total rainfall displayed lower CH_4 uptake when compared to months with lower average soil moisture and lower total rainfall (Fig. 2). The coefficient of variance (CV) for the average CH_4 flux based on 10 chambers in one measurement cycle ranged between 1.8 and 98.0 % with an average of $17.9 \pm 11 \%$ (SD) and was higher in periods of rapid changes in soil moisture levels reflecting changes in precipitation (Fig. 2).

At the AU-WOM site soil CH_4 flux was always negative, indicating CH_4 uptake all year round (Fig. 3). The measurement cycle means ranged between $-1.3 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$

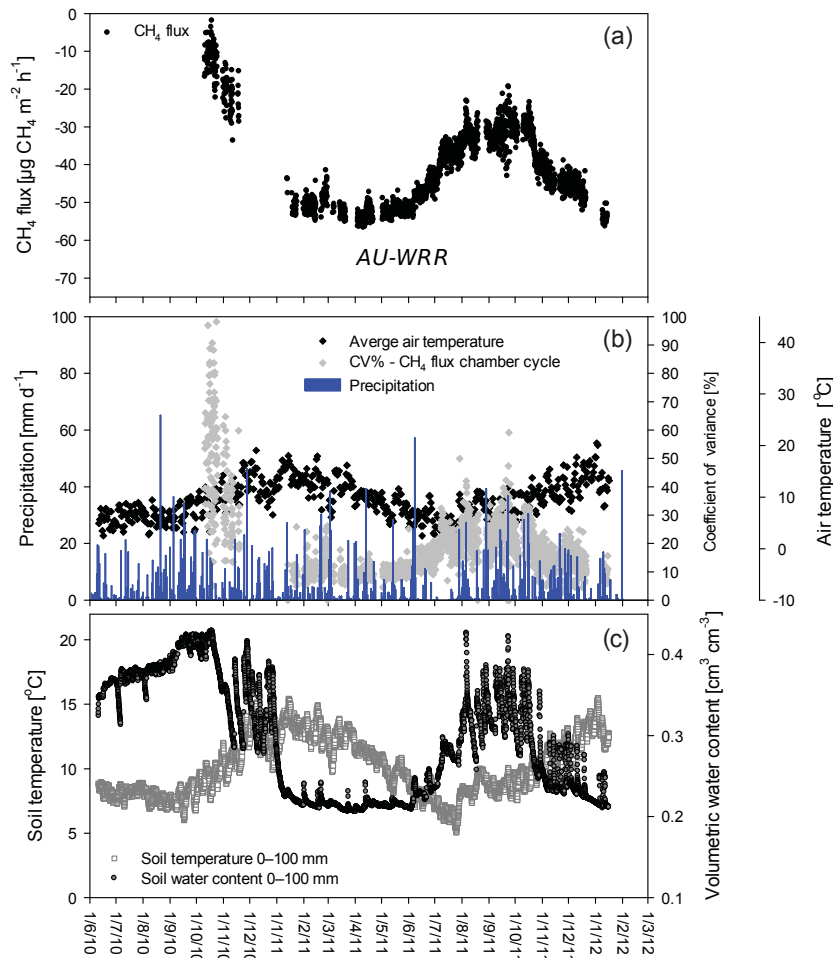


Figure 2. Soil-based flux of CH_4 at a mixed *Eucalyptus obliqua* and *E. regnans* forest stand. Warra LTER, Tasmania, Australia (AU-WRR). Panel (a) shows CH_4 flux cycle means of 10 chambers measured within a 4 h time period. Panel (b) shows site air temperature averaged over the chamber cycle period (black diamonds), daily rainfall sums (blue bars) and coefficient of variance of the CH_4 flux cycle mean shown in (a) (grey diamonds). Panel (c) shows soil temperature in the top 0–10 cm averaged over each chamber cycle (grey squares) and corresponding soil volumetric water content (black/grey circles) at the site.

(recorded during a period of heavy rainfall in summer 2011) to $-62.5 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ (summer 2010) with an arithmetic mean of $-25.5 \pm 12.7 \text{ SD } \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$. Similar to the AU-WRR site, months with higher average soil moisture and higher total rainfall displayed lower CH_4 uptake when compared to months with lower average soil moisture and lower total rainfall (Fig. 3). The CV for the average CH_4 flux based on six chambers in one measurement cycle ranged between 6.7 and 143.0 % with an average of $29.3 \pm 9.7 \%$ (SD) and was again higher in times of rapid soil moisture changes in response to changes in precipitation patterns (Fig. 3).

For AU-WRR the linear regression analysis showed that VWC accounted for approximately 85 % of variability in soil CH_4 uptake across all seasons (Fig. 4a, Table 1) with soil CH_4 uptake decreasing when soil VWC increased or soil CH_4 uptake increasing when AFP increased (Fig. 4b, Table 1). Soil temperature (0–5 cm) alone was weakly related

to CH_4 uptake with higher CH_4 uptake rates associated with higher soil temperatures. However, soil temperature alone was only able to account for approximately 16 % of seasonal variability in CH_4 uptake (Fig. 4c, Table 1). In addition, after taking the effect of VWC into account, soil temperature only explained around 1.5 % of the remaining variability in CH_4 uptake at AU-WRR (data not shown). A regression model containing VWC and soil temperature as input variables had only a marginally higher coefficient of determination when compared to the model only containing VWC (Table 1). Air-filled porosity or VWC showed some weak dependency of soil temperature at the site ($R^2 = 0.14$, $p < 0.001$).

For AU-WOM the linear regression analysis showed that VWC could account for around 91 % of variability in soil CH_4 uptake across all seasons (Fig. 4a, Table 1) with soil CH_4 uptake decreasing when soil VWC increased, the opposite trend was observed for AFP (Fig. 4b, Table 1). Soil tem-

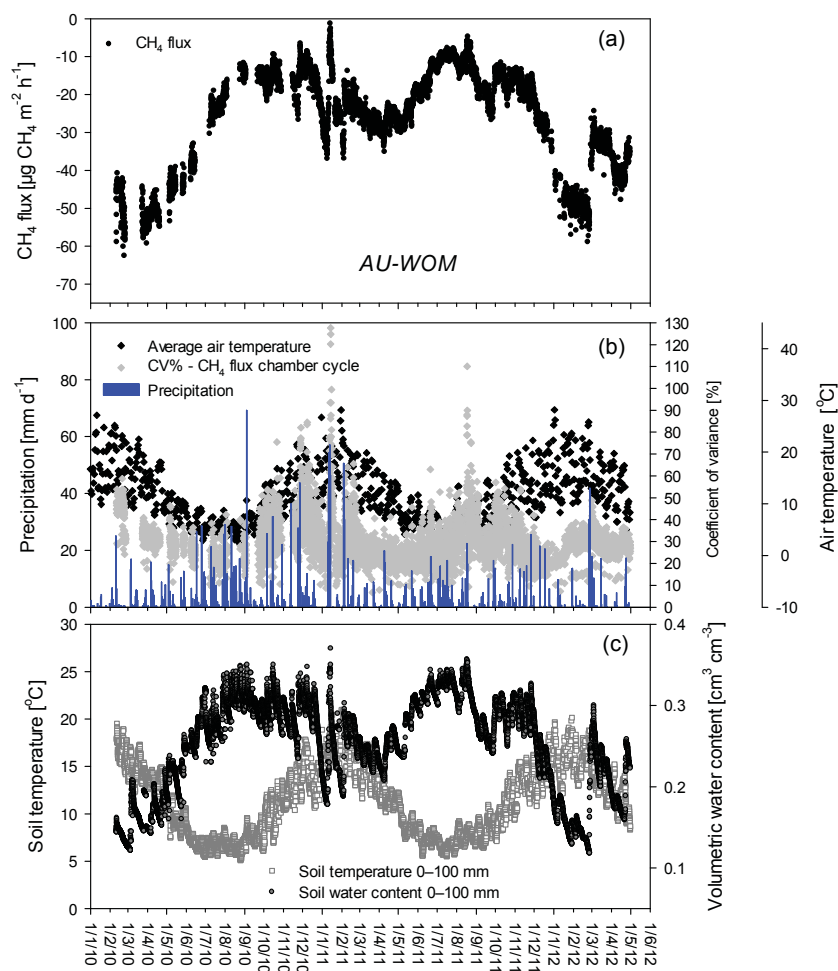


Figure 3. Soil-based flux of CH_4 at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria, Australia (AU-WOM). Panel (a) shows CH_4 flux cycle means of six chambers measured within a 2 h time period. Panel (b) shows site air temperature averaged over the chamber cycle period (black diamonds), daily rainfall sums (blue bars) and coefficient of variance of the CH_4 flux cycle mean shown in (a) (grey diamonds). Panel (c) shows soil temperature in the top 0–10 cm averaged over each chamber cycle (grey squares) and corresponding soil volumetric water content (black/grey circles) at the site.

Table 2. Parameters and coefficients of determination (Adj. R^2) of selected linear models in combination with results of a restricted maximum likelihood analysis (REML) explaining seasonal variability in mean chamber cycle methane flux (F_{CH_4}) at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria (AU-WOM) and at a mixed *E. obliqua* and *E. regnans* forest stand, Warra LTER, Tasmania, Australia (AU-WRR). Predictors: T_S (soil temperature) and AFP (air-filled porosity). REML results: Akaike information criterion (AIC); Estimate of importance for models containing both predictors are in parentheses.

Site	Dependent variable	Constant (intercept)	AFP (slope)	T_S (slope)	AIC	Adj. R^2
AU-WRR	F_{CH_4}	53.640	−195.378	–	5666	0.855
	F_{CH_4}	−19.543	–	−2.215	9657	0.158
	F_{CH_4}	55.587	−193.284 (0.997)	−0.254 (0.003)	5629	0.857
AU-WOM	F_{CH_4}	53.943	−195.768	–	7648	0.915
	F_{CH_4}	−6.320	–	−1.701	13 088	0.209
	F_{CH_4}	54.766	−201.671 (0.998)	0.147 (0.002)	7617	0.900

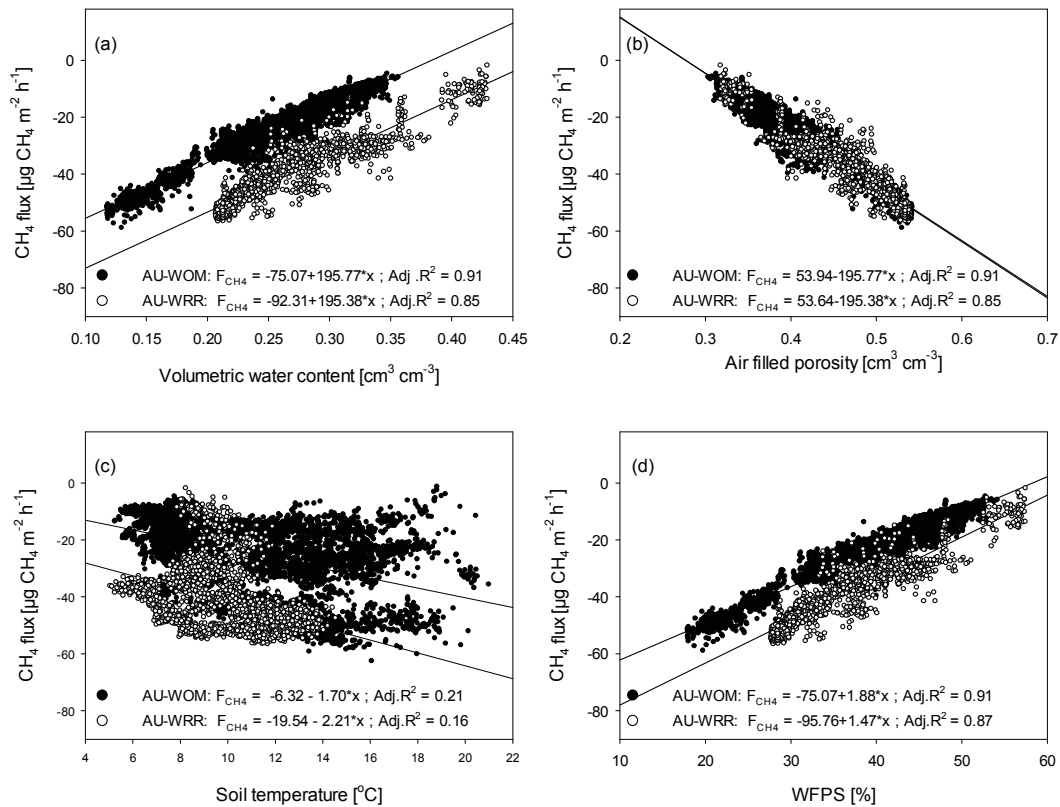


Figure 4. Relationships between soil volumetric water content and soil CH₄ flux (a), soil air-filled porosity and soil CH₄ flux (b), soil temperature and soil CH₄ flux (c) and soil water-filled pore space (WFPS) and soil CH₄ flux (d) for each chamber cycle at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria (black circles, AU-WOM) and at a mixed *E. obliqua* and *E. regnans* forest stand, Warra LTER, Tasmania, Australia (white circles, AU-WRR). Lines symbolise significant linear regressions between the parameters (regression parameters are listed in Table 1).

perature (0–5 cm) alone was again weakly related to CH₄ uptake with higher CH₄ uptake rates associated with higher soil temperatures (Fig. 4c). At the AU-WOM site, only around 20 % of seasonal variability in CH₄ uptake (Table 1) was explained by soil temperature. In addition, similar to the results at AU-WRR, after taking the effect of VWC into account, soil temperature only explained around 5 % of the remaining variability in CH₄ uptake at AU-WOM (data not shown). Furthermore, a regression model containing VWC and soil temperature had a marginally lower coefficient of determination (Table 1) when compared to the model only containing VWC (Table 1). Air-filled porosity or VWC showed some weak dependency of soil temperature at the site ($R^2 = 0.38$, $p < 0.001$).

The AIC results of the REML analysis confirm the results of the linear regression approach (Table 2) showing that soil moisture (in this case expressed as AFP) is the strongest predictor of soil CH₄ flux in both forest systems. The analysis shows that the models including soil moisture and soil temperature perform marginally better based on AIC compared to models including only soil moisture to predict soil CH₄ flux. However, the importance rating of the predictors

(soil moisture and soil temperature) clearly indicates that in both forest systems soil moisture dominates as it accounts for more than 99 % of the proportion of variance explained by the model compared to < 0.01 % proportion of the variance explained by soil temperature.

3.2 Mean daily and annual CH₄ flux in relation to environmental variables

3.2.1 Site AU-WRR

Daily site averages ranged between -0.12 and $-1.35 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ with an arithmetic mean of -0.98 ± 0.27 (SD) $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. The coefficient of determination for the regression analysis changed slightly when the regression analysis was calculated on daily means and VWC was able to account for up to 89 % in the observed variability in CH₄ flux (Table 3). The CV for the daily average site CH₄ flux ranged between 0.15 and 20.6 % with an average of 3.5 ± 3.33 % (SD) and was higher in periods of rapid changes in soil moisture levels. We calculated soil CH₄ flux averages for 3 days around the dates when soil

Table 3. Parameters and coefficients of determination (Adj. R^2) of linear regression models explaining seasonal variability in mean daily methane flux (F_{CH_4}) at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria (AU-WOM) and at a mixed *E. obliqua* and *E. regnans* forest stand, Warra LTER, Tasmania, Australia (AU-WRR). Standardised coefficients β are in parentheses; SD refers to standard deviation of parameter; level of significance ($* \leq 0.001$). Predictors: T_S (soil temperature), AFP (air-filled porosity) and soil VWC (volumetric water content). Presented constants are model intercepts and parameters represent the slopes for the predictor variables.

Site	Dependent variable	Constant	VWC (SD = 0.058)	T_S (SD = 2.02)	AFP (SD = 0.058)	Adj. R^2
AU-WRR	F_{CH_4} (SD = 0.273)	-2.165*	4.433* (0.947)	-	-	0.896*
	F_{CH_4} (SD = 0.273)	-0.459*	-	-0.052* (-0.388)	-	0.148*
	F_{CH_4} (SD = 0.273)	-2.167*	4.435* (0.947)	0.0001 (0.001)	-	0.895*
	F_{CH_4} (SD = 0.273)	1.164*	-	-	4.433* (-0.947)	0.896*
		Constant	VWC (SD = 0.055)	T_S (SD = 3.55)	AFP (SD = 0.055)	Adj. R^2
AU-WOM	F_{CH_4} (SD = 0.275)	-1.819*	4.771* (0.962)	-	-	0.924*
	F_{CH_4} (SD = 0.302)	-0.161*	-	-0.038* (-0.452)	-	0.203*
	F_{CH_4} (SD = 0.275)	-1.915*	4.956* (0.999)	0.004* (0.053)	-	0.926*
	F_{CH_4} (SD = 0.275)	1.152*	-	-	-4.771* (-0.962)	0.924*

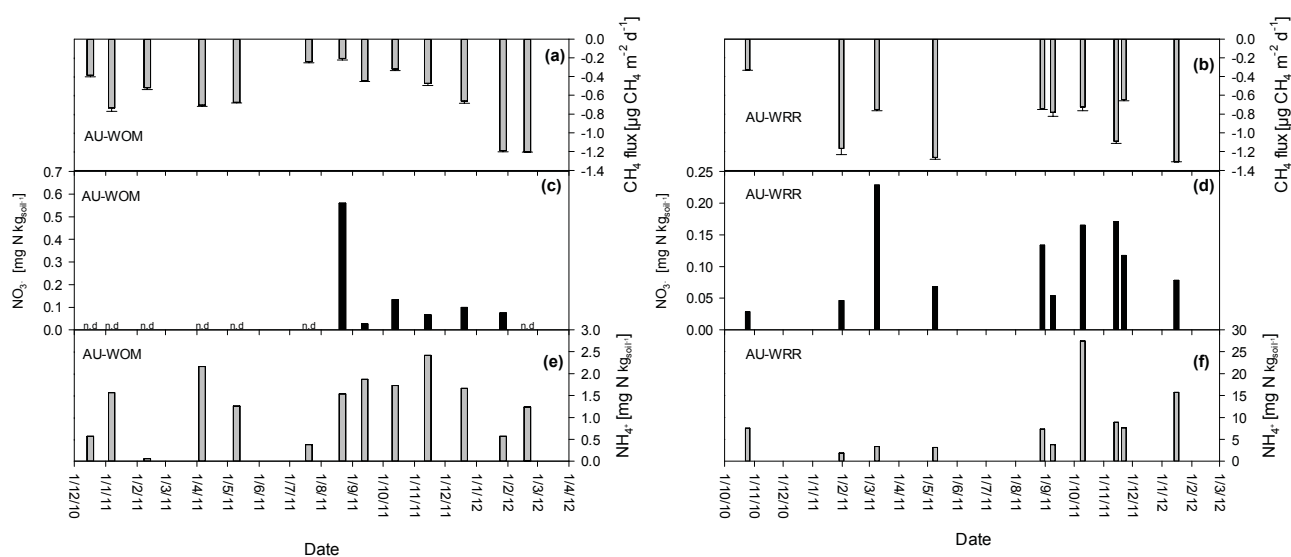


Figure 5. Dynamics in soil CH₄ flux (a, b) soil nitrate levels (c, d) and soil ammonium levels (e, f) at a mixed *Eucalyptus obliqua* forest stand, Wombat State Forest, Victoria (AU-WOM) and a mixed *E. obliqua* and *E. regnans* forest stand, Warra LTER, Tasmania (AU-WRR), Australia; n.d. means not detectable. Results of the linear regression analysis between CH₄ and NH₄⁺ or NO₃⁻ for both sites are not presented. They were AU-WOM: NO₃⁻ / CH₄ (Adj. $R^2 = 0.06$, $p = 0.21$) NH₄⁺ / CH₄ (Adj. $R^2 = -0.08$, $p = 0.83$); AU-WRR: NO₃⁻ / CH₄ (Adj. $R^2 = -0.11$, $p = 0.80$) NH₄⁺ / CH₄ (Adj. $R^2 = -0.11$, $p = 0.84$).

NH₄⁺ and soil NO₃⁻ samples were taken on-site to enable regression analysis; however, neither NH₄⁺ nor NO₃⁻ alone or together could explain any variability in soil CH₄ flux at the site and all relationships were non-significant (Fig. 5b, d, f).

3.2.2 Site AU-WOM

Daily site averages ranged between -0.11 and $-1.36 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ with an arithmetic mean of -0.62 ± 0.30 (SD) $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$. The CV for the daily

average site CH₄ flux ranged between 0.11 and 47.6 % with an average of 5.6 ± 4.36 % (SD) and was again higher in periods of rapid changes in soil moisture levels. As for the AU-WRR site the coefficient of determination for the regression analysis changed slightly when the regression analysis was calculated on daily means and VWC was able to account for up to 92 % in the observed variability in CH₄ flux (Table 3). Similar to the AU-WRR site, 3-day CH₄ flux averages were not significantly correlated with soil NH₄⁺ or NO₃⁻ if entered alone or together as predictors to the linear regression model (Fig. 5a, c, e).

3.3 Annual site CH₄ flux budgets

The calculated annual CH₄ budget for the year 2011 of the AU-WRR site was $-3.83 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$. The calculated annual CH₄ budget for the year 2011 of the AU-WOM site was $-1.79 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$.

4 Discussion

One of the most novel results of our study is the strong linear relationship observed between soil moisture and CH₄ uptake. To our knowledge the strength of this relationship is unique for temperate forest systems measured using continuous automated chamber systems over a long period. It is also striking that this strong linear relationship was similar in the two temperate eucalypt forests (dry and wet) regardless of the differences in forest structure, soil type, annual precipitation and geographical distance. It is possible that the two different measurement systems (GC at AU-WRR and FTIR at AU-WOM) could produce different measures of CH₄ flux if operated at the same site because of technological and methodological differences. If that were true, there would only be a remote chance that the two linear relationships between CH₄ flux and AFP would overlap one another. As such, our finding that the relationships between CH₄ flux and AFP do converge into one common regression line (as shown in Fig. 4) is worth noting and suggests similar accuracy between the two measurement systems and similar function in soil CH₄ exchange processes at the two forest sites.

CH₄ flux data collected in the long-term in temperate deciduous forest systems in Europe (Butterbach-Bahl and Papen, 2002) has shown that soil moisture can explain up to 58 % of the seasonality in soil CH₄ uptake. Similarly, Kiese et al. (2003) reported that soil moisture could explain up to 53 % of the seasonality in CH₄ exchange in a tropical rainforests in Queensland, Australia. Soil moisture influences soil gas diffusivity and is considered the most important factor controlling seasonality of CH₄ uptake in soils worldwide (Dalal et al., 2008; Dalal and Allen, 2008; Smith et al., 2003, 2000; Ball et al., 1997) and the negative relationship between soil moisture and soil CH₄ uptake reported in this study has been previously reported for other ecosystems (Hartmann et al., 2011; Stiehl-Braun et al., 2011; Castro et al., 1994; Price et al., 2003). This agrees with the theory that soil CH₄ uptake is mainly limited by diffusion in most forest ecosystems (Price et al., 2004) when the sites of microbial CH₄ oxidation are distributed through the surface soil (Stiehl-Braun et al., 2011) and the concentration gradient between soil and atmosphere, which drives the flux, is effectively constant (von Fischer and Hedin, 2007). However, previous field studies have never been able to demonstrate so conclusively the strength of the relationship (> 90 % variation explained) between AFP and soil CH₄ uptake and for two separate forest systems. To our knowledge the only other study where

similarly strong correlations between soil moisture and CH₄ uptake have been reported was for grassland soils under summer rainfall exclusion (Hartmann et al., 2011).

It is important to note that WFPS has commonly been used to model, or compare, soil CH₄ uptake in different ecosystems (Del Grosso et al., 2000). However, in our study this soil environmental variable was not as effective as AFP in explaining the observed CH₄ flux patterns at the two temperate forest sites. At an individual site level, the relationship between WFPS and CH₄ uptake had the same coefficient of determination as between AFP and CH₄ uptake; however, the slope of the relationship differed between the two forest sites (Fig. 4d). This suggests that WFPS is not the most suitable soil moisture metric to relate soil gas diffusivity to soil CH₄ flux when comparing sites or ecosystems. This is most likely due to the fact that WFPS is a proportional measure that relates VWC to the total soil porosity (Eq. 4); compared to AFP that is a direct expression of the air-filled pore volume in a given soil (Eq. 5).

This demonstrates that soil gas diffusivity is primarily related to the volumetric fractions of air (AFP), rather than the volumetric fraction of water in the soil since diffusion through air is much faster than through water (Farquharson and Baldock, 2008).

Our data also show a very weak influence by soil temperature on soil CH₄ uptake. This temperature effect appears to be mainly driven by the correlation between soil moisture and soil temperature, which is typical for the climate of the investigated forest systems. After the effect of soil moisture was accounted for, soil temperature was only able to account for less than 5 % of the remaining variability in soil CH₄ flux at AU-WOM and less than 1.5 % of the remaining variability in soil CH₄ flux at AU-WRR. Furthermore, the daily temperature variation in soil CH₄ uptake would have been masked in the analyses because all regression analyses were performed on either chamber cycle or daily uptake means. However, the overall weak but statistically significant temperature dependency of soil CH₄ uptake is unlikely to greatly influence seasonal CH₄ flux variability given that at both sites around 90 % of seasonal variability in CH₄ uptake can be explained by soil moisture alone and that soil moisture and temperature are weakly correlated in the investigated forest systems. This was more pronounced at the AU-WOM site because temporal soil moisture variability was greater and we had 2 years of data compared to 1 year of data at the AU-WRR site. However, a model that includes soil temperature and soil moisture together performed marginally better based on the AIC as compared to a model that only used soil moisture status in predicting soil CH₄ flux at both of our sites, which is logical based on the fact that all soil microbial processes show a physiological temperature response; but it appears that for the MOB, temperature response is rather muted at our sites during our measurement time frame. Furthermore, our data also show that soil CH₄ uptake still continued at a very low WFPS of 10 % ($\text{VWC} = 0.07 \text{ g cm}^{-3}$,

AFP = $0.59 \text{ cm}^3 \text{ cm}^{-3}$) with CH_4 uptake ranging between -62 to $-80 \mu\text{g CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ at this time. We can therefore hypothesise that MOB activity was not severely limited by moisture at the AU-WOM and the AU-WRR sites during the measurement period.

This study reports continuous measurement of soil-atmosphere CH_4 exchange in two temperate eucalypt forests in Australia measured at high-temporal resolution for >12 months. Mean daily CH_4 flux values (AU-WRR = -1.35 to $-0.12 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$; AU-WOM = -1.36 to $-0.11 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) were well within the reported range for other temperate forests in Europe (-2.47 to $+0.26 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$; Smith et al., 2000) or worldwide (-10.68 to $0.02 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$; Dalal et al., 2008; Dalal and Allen, 2008).

The estimated annual CH_4 uptake of $-1.79 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ for AU-WOM and $-3.83 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ for AU-WRR are comparable to the range of -2.5 to $-3.7 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ reported for temperate beech and spruce forest sites in Germany where CH_4 fluxes were measured with a similar automated system over multiple years (Butterbach-Bahl and Papen, 2002). Globally, a range of -1.31 to $-10.5 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ has been reported for temperate forest systems based on short- and long-term automated and manual chamber measurement campaigns (Dalal et al., 2008; Dalal and Allen, 2008). The annual CH_4 uptake rate estimated for AU-WOM in our study was less than a third of the $-5.8 \text{ kg CH}_4 \text{ ha}^{-1} \text{ yr}^{-1}$ estimated by Meyer et al. (1997) for soils in the same forest system. This earlier CH_4 sink estimate was based on only five seasonal flux measurements but might also be attributed to the measurements being taken during three dry years (1993–1995) when average rainfall was 677 mm yr^{-1} (Meyer et al., 1997). In comparison, the years when our study was undertaken (2010–2012), the average rainfall was 1063 mm yr^{-1} . This may partly explain the greater CH_4 uptake estimate of Meyer et al. (1997) as the lower soil moisture levels may well lead to greater CH_4 uptake rates.

5 Conclusion

Our field data suggest that the difference in magnitude of CH_4 flux at both sites was based solely on differences in AFP due to site differences in soil bulk density, soil porosity as a near-identical relationship between AFP and soil CH_4 uptake existed at both sites. This means that future research should investigate whether simple information about soil bulk density can be used to estimate CH_4 uptake across different eucalypt forest ecosystems in Australia, or in other similar ecosystems globally. Our data further demonstrate that temporal variability in soil CH_4 uptake was predominantly controlled by temporal variability in soil AFP that is linked to soil gas diffusivity. This means that seasonality in CH_4 uptake can be predicted with very high accuracy where

information about soil moisture dynamics is available or can be simulated with high certainty. However, since soil texture at both sites was relatively coarse and soils were both clay loams further studies need to establish if the AFP to CH_4 relationship holds true across different soil texture classes. Our results highlight the importance of long-term field measurements in establishing relationships between soil environmental drivers and soil CH_4 uptake and allowing the calibration of models used to calculate global CH_4 sink distribution and magnitude.

6 Data availability

The dataset can be accessed here: doi:10.4225/49/588574690c0ec (Fest, 2017).

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